THE CALIFORNIA SPECIES OF GUTIERREZIA (COMPOSITAE-ASTEREAE)

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The genus *Gutierrezia* (Compositae-Astereae) is represented in California by four species: *G. californica* Douglas, *G. bracteata* Abrams, *G.* sarothrae (Pursh) Britt. & Rusby, and *G. microcephala* (DC.) T. & G. (Solbrig, 1960). Of these four species, *G. microcephala* is fairly distinct and has been recognized in all the major floristic treatments. The other three species are closely related and their limits and identities have been considered differently in each of the major floristic treatments of California (Jepson, 1925; Abrams and Ferris, 1960; Munz, 1959). Since the characters distinguishing *G. bracteata* from *G. sarothrae* are not recognized easily in herbarium specimens and since there has been some doubt expressed in the past (Munz, 1935) as to the validity of these species, it was believed necessary to pursue the matter further by means of intensive field studies and population analyses. This report is an account of the results.

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Materials and Methods

This study is based on statistical analyses of wild populations, chromosome counts, garden investigations, hybridization experiments and herbarium specimens. Up to nine characters (height of plant, length and width of the involucre, number of ligulate and tubular flowers, length and width of achenes, length of pappus and pollen diameter) were measured in 50 plants chosen at random in each population studied. In this way, the value of different taxonomic characters could be evaluated in detail. Twenty populations were analyzed: two of *G. microcephala,* three each of *G. sarothrae* and *G. californica* and 12 of *G. bracteata*. Chromosome numbers were determined in a total of 25 populations. Two hundred pollen grains were measured in 16 populations of known chromosome number. Several collections were grown under uniform conditions at the Experimental Gardens of the University of California Botanical Gardens in Berkeley and later at the Harvard University Greenhouses in Cambridge, Massachusetts.

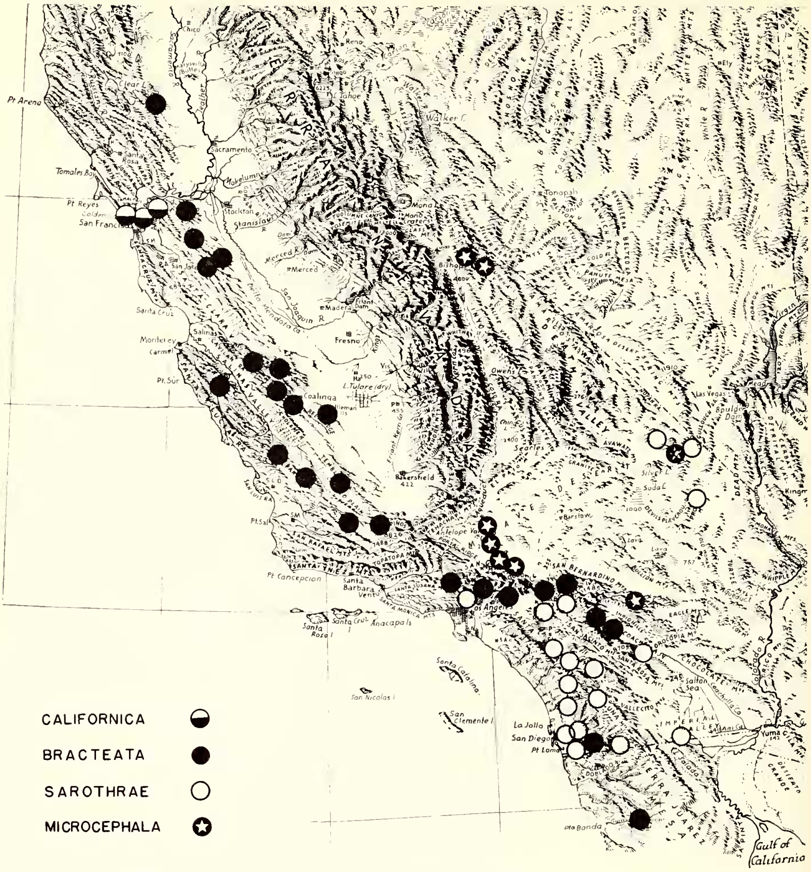

Fig. 1. Distribution of populations of *Gutierrezia* in California. (Base map Copyrighted by Ginn & Co., used by permission.)

Results

Distribution and ecological conditions. The most xerophytic of the California species of the genus is *G. microcephala*. It grows on the fringes of the Colorado and Mohave deserts on dry mountain slopes and in the valleys, but not in true desert areas (fig. 1). The more mesophytic *G. bracteata* and *G. sarothrae* have similar requirements. Both species are found in dry washes, rocky slopes and also occasionally in roadside ditches and in fields. *Gutierrezia bracteata* grows from Yolo Co. south along the drier parts of the Coast Ranges to northern Baja California; *G. sarothrae* is found only south of the Tehachapi Mts. all the way to southern Baja California, Cedros I. and west into the Great Basin and northern Mexico. *Gutierrezia californica* on the other hand is a species with narrow ecological requirements. It is found only on three serpentine outcrops in San Francisco Bay: one population on the Oakland Hills, one population on Angel Island, and one population on Point Bonita, Marin Co. Each of these three populations consists of less than 500 plants and all of them, but particularly the ones in Oakland and Marin Co., are threatened by encroaching civilization. Although *G. californica* is found in nature only on serpentine, it can be grown on non-serpentine soil without adverse effects. The same is true for progeny of the populations of *G. bracteata* which grow on serpentine soil.

Morphological analysis. a. Habit. The four species are similar in habit. All four are slightly woody subshrubs, semi- or completely globose, with small leaves and medium to small inflorescences borne at the end of the branches. *Gutierrezia californica,* which is significantly smaller than the rest, also conforms less to the habit description given, having a tendency to form only a few undivided and spreading branches which give rise to a rather open shrub. It also produces fewer inflorescences which tend to be borne solitary or on long stalks at the end of the branches. The other species form rather tight globose shrubs which are covered in the fall by small yellow heads which offer a rather showy display. *Gutierrezia bracteata* is probably the largest species, but the differences are not significant (table 1). When grown in the experimental garden, all four species maintained their characteristics but increased in size.

b. Inflorescence. It already has been stated that the capitula of *G. californica* are borne solitary or in loose groupings at the end of the branches. Those of *G. microcephala,* on the contrary, are found in tight glomerules of 3 to 8 sessile inflorescences. The disposition of the heads of *G. sarothrae* is similar to that of *G. microcephala* but there is often a short pedicel to each inflorescence while in *G. bracteata* as a rule the heads are borne on pedicels several millimeters long. There is, nevertheless, quite a bit of variability in this character.

There are differences in addition in the size of the capitula (table 1). The widest capitula are those of *G. californica* which vary from a population mean of 3.6 mm–4.20 mm; the narrowest are those of *G. microcephala* which average less than 1 mm wide. The capitula of *G. sarothrae* vary from an average value of 1.5 mm–2.5 mm per population while those of *G. bracteata* vary from 2.0 mm–3.4 mm. Although there is a slight overlap, it is clear that this last species tends to have wider heads. *Gutierrezia californica* also has the highest involucres (mean 5.70–7.50 mm average per population), but there is a sizable overlap with *G. bracteata* (mean 5.1–6.4 mm). *Gutierrezia sarothrae* (mean 3.4–4.4 mm) and *G. microcephala* (mean less than 3 mm) have shorter heads.

Populations of these four species can be separated on the basis of mean population values of these two capitulum parameters (figs. 2, 3). Not so individual heads which can deviate up to two times from the mean population size. Nevertheless, if an effort is made to sample average plants and to measure several heads, the capitulum furnishes one of the most valuable diagnostic characters.

Table 1. Mean Values for Plant Height, Height and Width of Involucre, Numbers of Flowers per Capitulum, Pappus Length and Pollen Diameter in Populations of California Gutierrezia

All values in mm with the exception of plant height which is given in inches. Numbers indicate Solbrig vouchers at GH and UC except two *G. californica* samples which represent mean values taken from herbarium specimens.

	Plant	Involucre		No. of Flowers		Pappus		Pollen
	Height	H.	W.	Lig.	Tub.	Lig.	Tub.	Diam.
G. californica.								
Point Bonita, *3431*	10.86	7.52	3.63	7.5	12.54	0.97	1.74	18.57
Angel Island herb. sample)	......	5.70	4.20	7.3	10.2	......	......	......
Oakland (herb. sample)	......	5.21	3.77	7.2	11.1	......	......	......
G. bracteata								
Cache Creek, *3432*	23.44	5.58	2.12	6.4	6.9	0.63	1.40	......
Arroyo del Puerto, *3433*	17.31	6.13	2.36	7.2	8.6	0.56	1.40	14.23
Arroyo del Puerto, *2743*	15.03	5.12	3.39	7.6	9.0	0.91	1.80	13.83
New Idria Rd., *3434*	17.85	6.19	2.19	5.9	6.5	......	......	......
New Idria, *3435*	16.48	5.86	2.15	......	......	......	......	......
New Idria, *2830*	......	......	......	......	......	......	......	16.18
Los Gatos Canyon, *3436*	22.58	5.75	2.05	......	......	......	......	15.99
Kettleman Hills, *3437*	24.34	6.34	2.15	......	......	......	......	......
Pond Ranch, *2748*	23.7	5.16	3.30	6.5	8.9	1.24	2.02	......
McKitrick, *3438*	18.89	5.88	2.24	......	......	......	......	......
Temblor Range, *2755*	18.53	5.57	2.61	4.9	4.3	0.98	1.75	......
Cuyamas Valley, *3439*	19.94	6.38	2.09	......	......	......	......	16.51
Los Angeles, *3440*	32.25	5.53	2.04	......	......	......	......	13.97
Tahquitz Canyon, *2775*	......	......	......	......	......	......	......	15.63
G. sarothrae								
Idylwild, *2773*	......	......	......	......	......	......	......	13.48
Temecula, *2758*	22.4	4.36	2.48	5.5	5.3	0.58	1.46	......
Aguanga, *2760*	......	......	......	......	......	......	......	13.90
SantaYsabel, *2763*	......	......	......	......	......	......	......	13.32
Santa Ysabel, *2765*	......	......	......	......	......	......	......	13.98
Rancho Santa Fe, *2769*	20.3	3.43	2.15	5.8	5.9	0.34	0.93	13.06
Chula Vista, *2768*	......	......	......	......	......	......	......	13.84
Chula Vista, *2766*	17.27	3.51	1.85	5.5	4.6	0.59	1.14	13.30
G. microcephala								
Hyde Park, Ariz., *2804*	12.6	3.6	1.00	1.0	1.0	......	......	......
White City, N.M., *3272*	10.4	2.5	0.80	0.9	1.0	......	......	......
St. David, Ariz., *2790*	17.8	......	......	......	......	......	......	......

c. Flowers. Two floral characters are of taxonomic significance: number of flowers per inflorescence and size of pappus, both for the ligulate and tubular flowers.

The largest number of flowers per capitulum is found in *G. californica*. The mean values per population are 7.2–7.5 ligulate flowers and 10.2–12.5 tubular flowers per capitulum. *Gutierrezia bracteata* follows with 4.9–7.6 ligulate and 4.3–9.0 tubular flowers; *G. sarothrae* has 5.5–5.8 ligulate and 4.6–5.9 tubular ones; while *G. microcephala* has almost consistently one ligulate and one tubular flower per head. As with the characteristics of the capitulum, *G. californica* and *G. microcephala* are fairly distinct, while *G. bracteata* and *G. sarothrae*, although differing, have an area of overlap (fig. 2). Also it has to be remembered that these are mean values. Individual heads may have an excess or deficiency of the numbers given and at least 10 capitula should be analyzed in order to obtain a fairly reliable value.

The pappus length follows the same pattern as the number of flowers in a head: *G. californica* has the largest pappus, *G. microcephala* the smallest; *G. bracteata* and *G. sarothrae* have similar values, although the figures for the former are slightly larger. The pappus furnishes a valuable additional character.

d. Pollen size. The pollen diameter of populations of *G. sarothrae*, *G. bracteata* and *G. californica* of known chromosome number was measured. The results are represented graphically in Fig. 2. Although there is a correlation between chromosome number and pollen diameter, the distribution is a continuous one. The variability exhibited by *G. bracteata* in this character is worth noting.

Chromosome number. The California populations of *Gutierrezia* counted to date are listed in Table 2. All populations of *G. sarothrae* had n = 4, those of *G. microcephala* n = 8 and those of *G. californica* n = 12. So far only one number has been found in each population, but not more than five plants have been sampled per population. All the populations of *G. bracteata* with n = 12 are found on the south Coast Ranges while populations with n = 8 are found throughout the range of the species. No obvious morphological difference could be found in the chromosomes of the various species (Rüdenberg and Solbrig, 1963).

Hybridization attempts. Plants of *G. sarothrae*, *G. californica* and *G. bracteata* (n = 8 and = 12) were intercrossed in Berkeley in 1957 and 1958 (Solbrig, 1960) and again in Cambridge in 1960 and 1961. All these attempts except one were unsuccessful. An interspecific hybrid was obtained between *G. californica* and *G. bracteata* (n = 8), but was completely sterile (loc. cit.). Although normally outbreeding, the plants of *Gutierrezia* are self-compatible; this hinders artificial hybridization attempts considerably. The results therefore are not as conclusive as could be wished, but apparently the species are fairly intersterile. In view of the differences in chromosome number this result is not surprising.

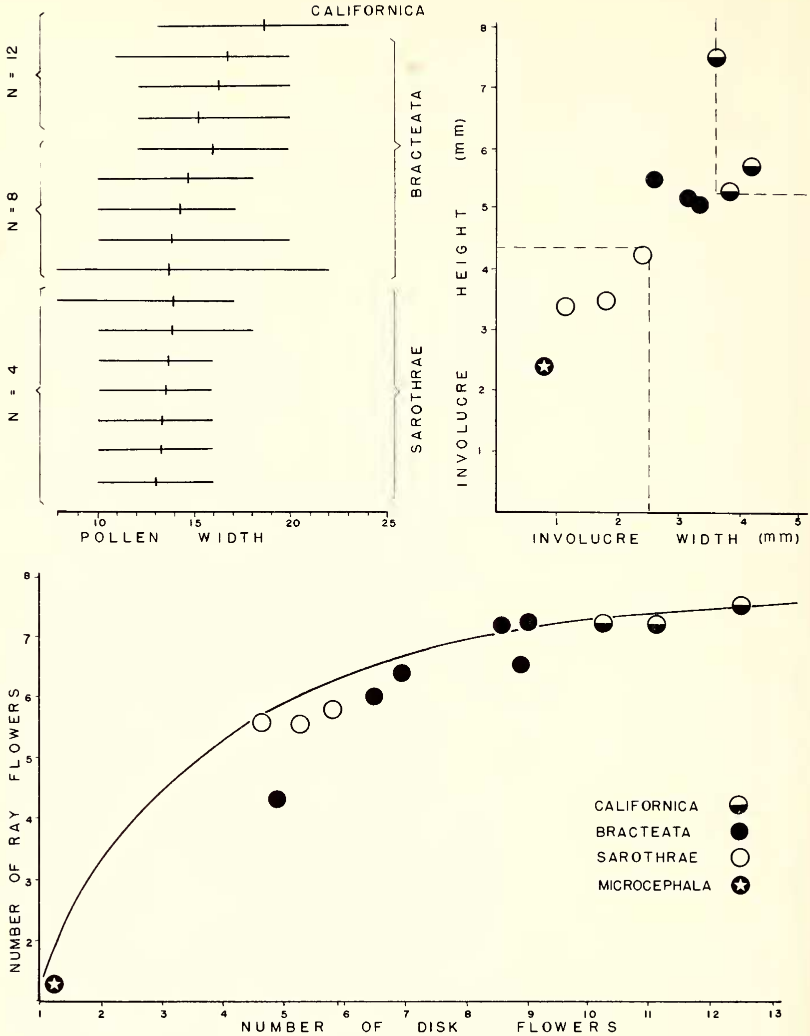

FIG. 2. Graphs showing correlation of pollen diameter (in micra) and chromosome number (horizontal bar = range; vertical bar = mean); mean population width and height of the involucre (in mm); and mean number of disk and ligulate flowers in a head.

DISCUSSION

The taxonomic problem. Viewed from the vantage point of good knowledge of the species in the field and after carefully analyzing a number of breeding populations, the species appear fairly distinct. The same cannot be said, unfortunately, when the problem at hand is the

Table 2. Chromosome Numbers in California Species of Gutierrezia

G. californica. **n = 12.** Contra Costa Co., Oakland Hills, *Solbrig 2154.* Marin Co., Angel Island, *Solbrig 2681;* Point Bonita, *Solbrig3431.*

G. bracteata. **n = 8.** Yolo Co., Cache Creek, Rancho S. Ana Bot. Garden seed. Alameda Co., Corral Hollow, *Solbrig 2159.* Stanislaus Co., Patterson, *Solbrig 2743, 3433.* San Benito Co., Los Gatos Canyon, *Solbrig 3436.* San Luis Obispo Co., La Panza, *Solbrig 2751.* Los Angeles Co., Tujunga, Wash., *Solbrig 3440.* **n = 12.** San Luis Obispo Co., Temblor Range, *Solbrig 2753.* Santa Barbara Co., Padres Nat. Forest, *Solbrig 2167;* Cuyama Valley, *Solbrig 2166, 3439.* Riverside Co., Idylwild, *Solbrig 2774.* San Benito Co., New Idria, *Solbrig 2830.* San Bernardino Co., Tahquitz Canyon, *Solbrig 2775.*

G. sarothrae. **n = 4.** Riverside Co., Idylwild, *Solbrig 2773.* San Diego Co., Agul anga, *Solbrig 2760;* Temecula, *Solbrig 2758;* Santa Ysabel, *Solbrig 2763, 2765;* Rancho Santa Fe, *Solbrig 2769;* Chula Vista, *Solbrig 2766, 2768.*

G. microcephala. **n = 8.** Inyo Co., White Mts., Rancho S. Ana Bot. Garden seed *9389.* San Bernardino Co., Morongo, Rancho S. Ana Bot. Garden seed *8382.*

identification of herbarium specimens, particularly incomplete or "scrappy" ones with poor or no label annotations. *Gutierrezia californica* and *G. microcephala* can be separated easily on the basis of involucral size and number of flowers per capitulum. On the other hand, large specimens of *G. sarothrae* and small ones of *G. bracteata* are likely to be confused. The characters used here offer the highest probability of correct identification, but the only absolute character is the chromosome number which obviously cannot be obtained from a herbarium specimen. A key to identify the California species of *Gutierrezia* follows.

Key to California species of Gutierrezia

Involucre 3.5 mm wide or more; tubular flowers more than 10; ligulate flowers more than 7. Plants of the San Francisco Bay area..1. *G. californica*

Involucre less than 3.5 mm wide; tubular flowers less than 9; ligulate flowers less than 7.

- Involucre 1.5 mm wide or less; 2.5 mm high or shorter; ligulate flower 1; tubular flower 1. Plants of the fringes of the Mohave and Colorado deserts and the White Mts..2. *G. microcephala*
- Involucre 1.5 mm wide or more; 3.0 mm high or more; ligulate flowers more than 4; tubular flowers 3 or more.
  - Involucre 2–3.5 wide; 5–7 mm high; ligulate flowers 5–7; tubular ones 4–9. Plants of the Coast Ranges and southern California....................3. *G. bracteata*
  - Involucre 1.5–2.5 mm wide; 3.5–4.5 mm high; ligulate flowers 4–6; tubular one 3–6. Plants of southern California..4. *G. sarothrae*

A second taxonomic question is if populations of *G. bracteata* with n = 8 and n = 12 merit recognition as distinct taxa. The morphological analysis does not show any appreciable difference but the crossing attempts seem to indicate that they are intersterile as expected. The situation of *G. bracteata* is not unique in the genus; polyploid populations of *G. sarothrae* (Solbrig 1960; 1964) and of *G. microcephala* (Solbrig, 1960) are also known. Even though there might be some merit in giving taxonomic recognition to these genetically isolated populations

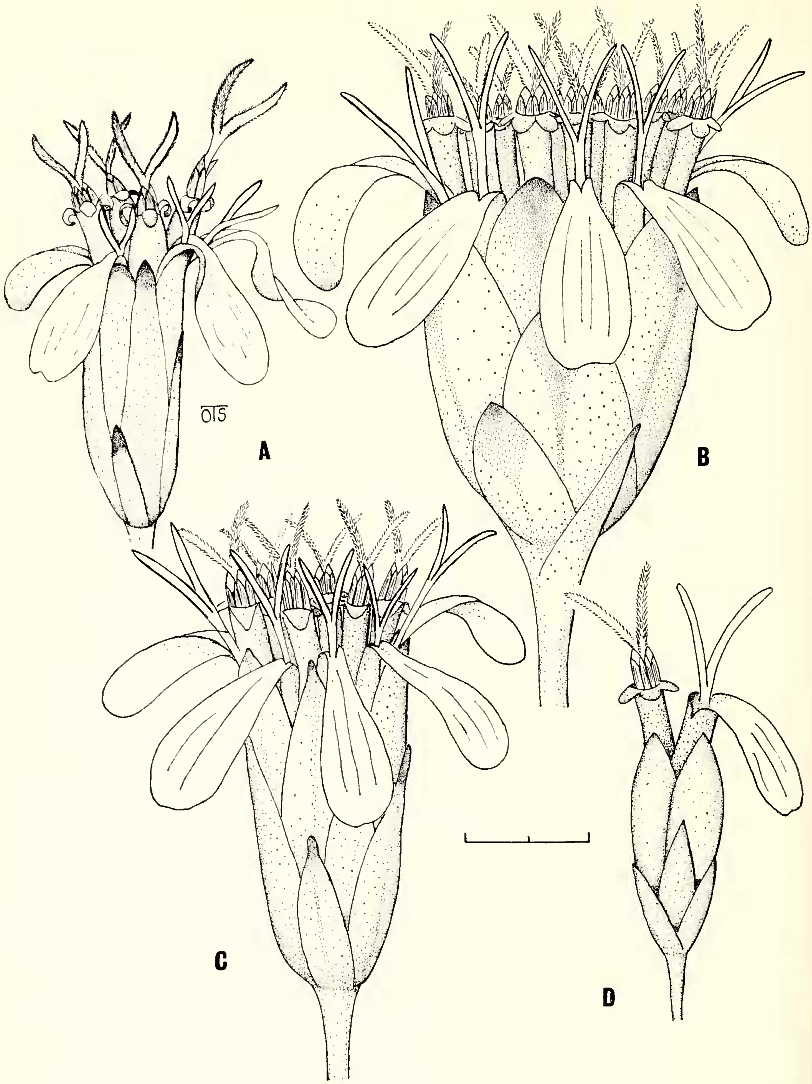

FIG. 3. Capitula of the four species of *Gutierrezia:* A, *G. sarothrae;* B, *G. californica;* C, *G. bracteata;* and D, *G. microcephala.*

(in reality sibling species), I prefer not to. In the absence of any absolute morphological difference (no matter how small), it serves, in my opinion, no practical purpose.

Evolutionary history. Any statement about the evolutionary history of these species is highly speculative since there is no direct paleobotanical evidence. Nevertheless this much seems clear. The genus *Gutierrezia* represents a polyploid complex with a base number of x = 4 and speciation has taken place by increases in chromosome number together with ecological specialization. Of the living species, *G. sarothrae* is the most primitive one and is probably not much differffent from the ancestral stock (Solbrig, 1964, and in prep.), which was probably native to the lower central basin or to northern Mexico. It is clear from the morphological analysis and geographic distribution that there were at least two invasions of *Gutierrezia* into California. One was by *G. sarothrae* and the other by *G. microcephala*. This latter species is probably of more recent arrival, both on account of its highly specialized type and also because it occupies a habitat which is relatively recent in California (Axelrod, 1950; 1956). The range of *G. sarothrae* might have once been continuous between the central basin and its present California distribution, continuity which was interrupted by the formation of the Mohave and Colorado deserts in late Pliocene age. The presence of isolated populations of *G. sarothrae* in the New York Mts. seems to indicate so. The species might have also extended once north along the coast ranges, although I have no indication of this. But it is tempting to speculate that this hypothetical continuous range was broken by the invasion of the sea into the Cuyama and Central Valley in the late Miocene and early Pliocene (Axelrod, 1956; James, 1963). The isolated populations to the north could have then evolved into n = 8 *G. bracteata*. Secondary contact after the retreat of the water in late Pliocene or Pleistocene might have produced n = 12 *G. bracteata* through amphiploidy. The tetraploid populations of *G. bracteata* might be the result of autopolyploidy followed by selection in the manner postulated by Darlington (1956), or they may be the result of amphiploidy with a now extinct species. This last pattern would be more in accordance with what is observed in other polyploid complexes (Stebbins 1950; and pers. comm.), nevertheless the close morphological similarity between *G. sarothrae* and *G. bracteata* does not rule out the first explanation.

The origin of *G. californica* is equally obscure, but it probablv diverged from *G. bracteata,* by rapid evolution after moving into the slightlv more humid climate of the San Francisco Bay area. If the evolution of *G. californica* was the result of isolation or of hybridization of a tetraploid *G. bracteata* with an extinct diploid species cannot be determined. Nevertheless, the absence of known hexaploid *G. bracteata* north of San Benito Co., the morphological distinctness of *G. californica* and the pattern of behavior of other polyploid complexes appear to favor the hybridization hypotheses.

A point worth mentioning is the adaptation of populations of *G. bracteata* and *G. californica* to serpentine soils. The first of these species is not quite a true serpentine species. In every instance, the populations are found on soil fairly mixed with materials derived from other types of rocks. This can be observed best in the large serpentine outcrops in New Idria.

On the other hand *G. californica* is a true serpentine endemic. Kruckeberg (1954) has discussed some genetic aspects of serpentine adaptation in particular reference to the genus *Streptanthus*. *Gutierrezia californica* can be grown on regular soils, but apparently cannot withstand competition in such soils in a natural situation. Plants of *G. bracteata* from non-serpentine localities can grow on serpentine, but they do better on other soils. They can, nevertheless, be considered preadapted to serpentine. In the San Francisco Bay area, the only suitable habitats available for *G. bracteata* plants were probably the serpentine outcrops. After that, isolation together with selection and genetic drift can be accounted to have brought forth a faster rate of evolution.

Gray Herbarium, Harvard University

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